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The Adult Behavior of the Japanese Cabbage White (Lepifoptera, Pieridae) in the Field

II. Ecological Aspects of Major Behavior Patterns

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Synopsis Major adult behaviors of *Pieris rapae crucivora* BOISDUVAL were analyzed functionally and their ecological topics were picked up (11 sectional conclusions), based on the field observation by 'single-individual trailing method'. *Resting, nectar intake, flying, egg laying* and interindividual behaviors were different sexually, seasonally and/or age-dependently. In interindividual behaviors, especially, functions of *ascending fight* and *abdomen erecting* were inferred with relation to age and/or population density, and functions of *fluttering, wing folding* and *leaning* which become effective during copulation as well. Based on 11 sectional conclusions, it was made clear that males continued to seek females which need males only once, and that consequently males drive females away out of home habitat.

Introduction

The Japanese cabbage white, *Pieris rapae crucivora* BOISDUVAL is one of the most abundant butterfly in Japan. An open behavioral catalog of the adult was reported in the previous paper (OHTANI, 1985). Based on it, we report here the ecological and functional aspects of the major behavior¹⁾.

The method adopted in this study can be called 'longitudinal' field observation (the continulus chasing of a marked individual), which offered us ecologically detailed informations, being different from the 'cross-sectional' field observation (time-spot one of many marked individuals) (*cf.* OHSAKI, 1979, 1980 ; YAMAMOTO, 1981a, 1983b ; *etc.*).

By our 'single-individual trailing method', we could observe some events happening to an individual, and record each event on the time-scaled sheet as the change of each behavior pattern. The event itself is the actual spot of 'the struggle for existence' of the butterflies in an ecological environment. Consequently, we could get

¹⁾ A list of the behavior patterns by OHTANI (1985) is shown in Table 1.

some ecological informations with a qualitative certainty. They are often quantitatively poor, but each of them might play the role in a trigger for more precise investigations.

Table 1. A list of behavior patterns with abbreviations after OHTANI (1985).

UNIT BEHAVIORS	
SOLITARY BEHAVIORS	INTERINDIVIDUAL BEHAVIORS
Resting (Re) } Hanging (Ha) } Inactivity (IN) Sleeping (Sl) }	Fluttering (Ft)
Self-cleaning (Sc)	Taking-off (To)
Head rolling (Hr)	Wing folding (Wd)
Walking (Wa)	Leaning (Le)
Nectar intake (Ni) } Water intake (Wi) } Feeding (FE)	Abdomen erecting (Ae)
Excreting (Ex)	Asending flight (Af)
Female-searching flight (Ff) } Laying flight (Lf) } Escaping flight (Ef) } Flying (FL) Wandering flight (Wf) } Roost-searching flight (Rf) }	Chasing gyration (CG) { Chasing (Ch/) Being chased (/Ch) Gyrating (Gy)
	Swarming (Sw)
	Prenuptial flight (Pf)
	Type-1 (Pf-1)
	Type-2 (Pf-2)
TEMPORALLY INTEGRATED BEHAVIORS	
Egg laying (El)	Mating (Mt)
Laying flight (Lf)	Prenuptial flight (Pf)
Drumming (dr)	Keeping closed (kc)
Pressing abdominal tip (pr)	Paralleling (pa)
Oviposition (ov)	Catching wings (cw)
	Grasping genitalia (gg)
	Nuptial flight (nf)
	Copulation (co)
	Pair-bond flight (bf)

Material and Methods

Study area

We observed adult behavior in the campus of Hokkaido University (Fig. 1) which consists of 3 important vegetations for the butterfly ; crop fields, abandoned areas with weeds, and patches of wood (cf. YAMAMOTO, 1981b). In abandoned areas and among crop fields, there are a lot of bushes of the exotic mustard, *Rorippa sylvestris* which is the main foodplant for larvae of *Pieris rapae crucivora* and *P. napi nesis* (cf. YAMAMOTO, 1981b).

We changed the releasing point (Fig. 1, A to B) of marked individuals with a reason for cultivation of the Farm (College Experiment Forests, Hokkaido Univ.), on 5 July in 1976.

Additional data on mating behavior (cf. Table 11) were obtained at the same campus in 1980, and at the 2 cabbage fields in Tabira-chô (Nagasaki Pref., northern Kyushu) in 1981.

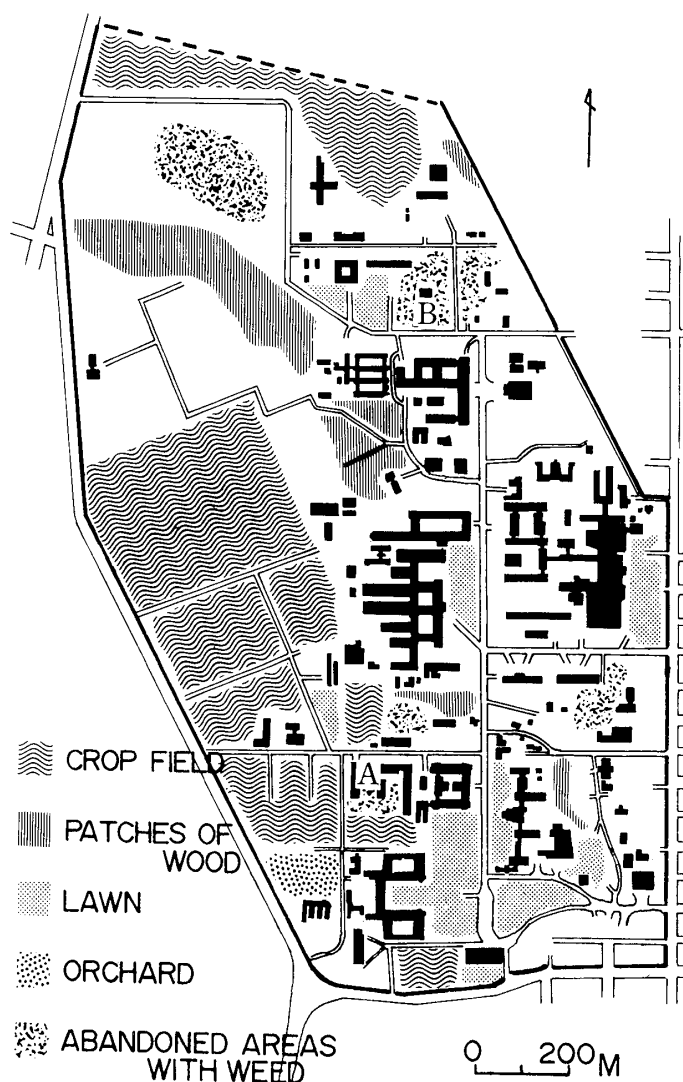


Fig. 1. Study area, the campus of Hokkaido University. A. First releasing point from April to June ; B. Second one from July to September. All buildings (black) are lower than 20 m.

Table 2. Individuals observed continuously. Question marks mean uncertainty. Ages with question marks were assumed on the basis of physical condition of individuals wings. The ages of 4 females (♀20, ♀21, ♀23h, ♀17) were based on our observations that females mated with males within a day since emergency (except early spring).

Individual code	Generation	Days observed		Total hours observed	Observation started from	Caught in
		Age	Date			
♀2	h	7-9	Apr. 25-27	16.6	virgin	pupa
♀1	h	4(?)	May 9	1.9	mated	adult
♀10h	h	1,2	May 9,10	8.4	virgin	pupa
♀13	h	2(?)—4(?)	May 13-15	14.0	mated	adult
♀15	h	3(?), 4(?)	May 19,10	6.2	mated	adult
♀20	h	2,13-16	May 27, Jun. 7-10	14.0	mating	adult
♀21	h	1,2	May 27,28	4.4	mating	adult
♀23h	h	2	May 29	4.0	mating	adult
♀22h	h	2,4	May 30	2.5	mated	pupa
TOTAL (9 females)-----				72.0		
♀3	1	2,3	Jun. 25,26	14.5	virgin	pupa
♀4	1	2	Jun. 30	6.0	virgin	pupa
♀5	1	3-5	Jul. 1-3	25.6	virgin	pupa
♀10	1	1-3	Jul. 6-8	17.1	virgin	pupa
♀17	1	2-8	Jul. 12-18	25.4	mating	adult
♀22	1	2,3	Jul. 18,19	5.8	mated	pupa
♀23	1	7,8	Jul. 23,24	12.8	mated	pupa
TOTAL (7 females)-----				107.2		
♀26	2	4,5	Jul. 29,30	20.4	mating	pupa
♀41	2	1,2	Aug. 6,7	17.9	mating	pupa
♀50	2	1(?)	Aug. 14	3.0	?	adult
♀47	2	10-19	Aug. 17-26	51.0	mated	pupa
TOTAL (4 females)-----				92.3		
♂3	h	2(?)—6(?)	Apr. 28 - May 2	11.8	?	adult
♂8	h	3(?)—8(?)	May 3-8	19.1	?	adult
♂12h	h	2	May 11	2.2	unmated	pupa
♂16	h	6	May 24	4.9	?	pupa
TOTAL (4 males)-----				38.0		
♂7	1	4	Jul. 4	5.7	?	pupa
♂12	1	2-4	Jul. 9-11	18.1	unmated	pupa
♂24	1	1-3	Jul. 19-21	20.4	unmated	pupa
♂11	1	15, 16	Jul. 21,22	2.4	?	pupa
TOTAL (4 males)-----				46.6		
♂27	2	3-7	Jul. 31 - Aug. 4	33.9	unmated	pupa
♂45	2	8,21-23	Aug. 14,27-29	12.9	?	pupa
♂29b	2	18(?)—20(?)	Aug. 15-17	11.9	?	adult
TOTAL (3 males)-----				58.7		
GRAND TOTAL (31 individuals)				414.8 (♀♀: 271.5; ♂♂: 143.3)		

h: post-hibernating generation; 1: first one; 2: second one

Butterflies

In Sapporo, *Pieris rapae crucivora* produces 3 generations per year; the post-hibernating generation (G_h) in May to June, the first one (G_1) in July and the second one (G_2) in August. Relative abundance of adults per day is $G_h \ll G_2 < G_1$ on the campus of Hokkaido Univ. (cf. YAMAMOTO and OHTANI, 1979; YAMAMOTO, 1981b).

Individually marked adults (11 males and 20 females) were observed in 1976. Table 2 shows the details of observed individuals. The data of older individuals were often omitted because of a poor number of individuals observed for the analysis.

Observation

We adopted the 'single-individual trailing method': we release one marked individual, trail it at the distance of several meters¹⁾, check all the behaviors of it (often by a binocular) on the time-scaled data-sheet and continue the observation day after day. After it died or disappeared, the same method was repeated for other marked adults.

Results and Discussion

Ecological or functional aspects of 7 behavior patterns are described and discussed here. The sectional conclusions are condensed in 11 successive summaries (S-1 to S-11) which are given by italics in the text. They are referred to General Discussion.

1. Resting (Re)²⁾ and resting site

There is a little difference in the distribution pattern of the duration of *Re* between sexes (MANN-WHITNEY's U-test and Two-sample median test³⁾, not significant).

The plants and other objects used for resting sites are shown in Table 3. In spring ($=G_h$), when the plant cover was still poor, 4 plant species were frequently used (*Petasites japonicus*, *Rorippa sylvestris*, *Erigeron annuus* and *Remex obtusifolius*). Among them *Petasites* was more frequently used by males than by females, while *Rorippa* vice versa. The number of plant species for resting site increased from spring to summer in parallel with the seasonal enrichment of vegetation.

There was a sexual difference in plant preference; females preferred oviposition plants (*Rorippa*, *Raphanus* and *Sisymbrium*) for resting sites more than males did. On the other hand, males more frequently visited the second group of plants in Table 3 than females. *Artemisia*, *Phytolacca*, *Solanum*, *Cirsium* and *Petasites* have leaves with whitish undersides.

In this connection, the color difference between *Chenopodium album* and *C. album* var. *centrorubrum* should be mentioned. The undersides of leaves of both varieties are whitish, but the upperside of *centrorubrum* wears reddish powdery hair, while that of *album* whitish one. The former was commoner and visited by both sexes, whereas *C.*

¹⁾ Trailing without disturbing its behavior was shown by ROOT and KAREIVA (1984) who compared with the behavior observed from top of two 10-m towers.

²⁾ *Re* includes 'sun-bathing' and 'sun-avoiding' (cf. OHTANI, 1985)

³⁾ cf. ISHII (1975), pp. 107-109.

Table 3. The number of cases (N) and its percentage observed on plants and other objects used for resting sites.

Plants	Post-hibernating generation (G _h)			First generation (G ₁)			Second generation (G ₂)		
	Height (cm)	N	%	♀	N	%	Height (cm)	N	%
Plants for oviposition									
<i>Rorippa sylvestris</i>	5-30	45	17.6**	0	0.0**				
<i>Sisymbrium officinale</i>	5-40	41	16.1**	0	0.0**				
<i>Brassica campestris</i>	5-30	1	0.4	0	0.0				
<i>Raphanus raphanistrum</i>	5-20	0	0.0	0	0.0				
<i>Armoracia rusticana</i>	5-30	3	1.2	0	0.0				
Plants with whitish leaves (underside)									
<i>Chenopodium ficifolium</i>	1-10	21	8.2**	36	26.2**				
<i>C. album</i>	5-20	0	0.0	0	0.0				
<i>C. a. var. centrurubrum</i>	5-20	0	0.0	0	0.0				
<i>Solanum nigrum</i>	1-10	0	0.0	0	0.0				
<i>Petasites japonicus</i>	30-45	15	5.9**	30	21.9**				
<i>Phytolacca esculenta</i>	20-50	2	0.8	5	3.6				
<i>Artemisia vulgaris</i> var. <i>vulgatissima</i>	10-50	4	1.6	1	0.7				
<i>Cirsium arvense</i> var. <i>setosum</i>	5-20	0	0.0	0	0.0				
Other plants									
<i>Erigeron annuus</i>	10-30	20	7.8	6	4.4				
<i>Solidago altissima</i>	30-50	9	3.5	2	1.5				
<i>Helianthus tuberosus</i>	30-50	0	0.0	2	1.5				
<i>Rumex obtusifolius</i>	5-30	14	5.5	14	10.2				
<i>Taraxacum officinale</i>	5-30	6	2.4	1	0.7				
<i>Plantago asiatica</i>	5-20	1	0.4	0	0.0				
Dicotyledoneae spp.		23	9.0*	3	2.2*				
Monocotyledoneae spp.		7	2.7	4	2.9				
Dead leaves		23	9.0	23	16.8				
Stones and soil		86	33.7	46	33.6				
Total		255	100.0	137	100.0				
No. spp. of plants (♀:64; ♂:47)		26**		10**					
No. spp./individual (♀:11.7; ♂:12.0)		8.2		6.0					

Significantly different between sexes: *P<0.05; **P<0.02; ***P<0.01; ****P<0.001

Table 4. Sexual difference in the height of resting sites preferred by 2 marked adults.

Individual	Plant used as resting site	Height above the ground (cm)																	Total
		0	1	3	5	6	7	8	9	10	12	15	20	30	40	50	90		
♂45	<i>Zoysia japonica</i>	1	1															2	
	<i>Trifolium repens</i>			1		1												2	
	<i>Chenopodium ficifolium</i>									1								1	
	<i>Artemisia vulgaris</i> var. <i>vulgatissima</i>										1	1						2	
	Gramineae sp.											1	1					2	
	<i>C. album</i> var. <i>centrorubrum</i>							1				2	1	1	3	4	1	13	
	<i>Lactuca Scariola</i>														1			1	
	<i>Helianthus tuberosus</i>													1	1	1		3	
	<i>Xanthium Strumarium</i>															1		1	
	Total (9 spp.)	1	1	1		1		1		1	3	3	3	5	6	1		27	
	Average height – 30.2* cm																		
♀47	Gramineae spp.		1															1	
	<i>Plantago asiatica</i>	1	2		2													5	
	<i>Taraxacum officinale</i>				1													1	
	<i>Angelica Miqueliana</i>				1													1	
	<i>Dactylis glomerata</i>				1													1	
	<i>C. album</i> var. <i>centrorubrum</i>	1		3	1	1	1		1									7	
	<i>Rorippa sylvestris</i>						1											1	
	<i>Rudbeckia laciniata</i>							1										1	
	<i>Paspalum</i> sp.								1									1	
	<i>Rumex obtusifolius</i>										1							1	
	Total (10 spp.)	2	3		8	1	2	1	2	1								20	
	Average height – 5.2* cm																		

*X²-test, P<0.001

Table 5. Observed cases of flower visits (V) and total durations (D) of *nectar intake* (Ni).

	G _h				G ₁			
	V		D		V		D	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
<i>Raphanus raphanistrum</i>	0	0	0	0	336 (30.6)* ²	37 (14.6)* ²	2805 (8.1)	575 (8.9)
<i>Rorippa sylvestris</i>	2 (1.6)	0	30 (0.4)	0	165 (15.0)	54 (21.3)	5450 (15.7)	765 (11.8)
<i>Brassica campestris Napus</i>	0	0	0	0	38 (3.5)	21 (8.3)	915 (2.6)	300 (4.6)
<i>Sisymbrium officinale</i>	0	0	0	0	0	1 (0.4)	0	25 (0.4)
<i>Armoracia rusticana</i>	0	0	0	0	1 (0.1)		10 (0.3)	
Total (oviposition plants)	2 (1.6)	0	30 (0.4)	0	540 (49.2)	113 (44.5)	9180 (26.5)	1665 (25.7)
<i>Taraxacum officinale</i>	87 (68.0)	48 (81.4)	4575 (61.9)	2655 (80.3)	125 (11.4)	47 (18.5)	9235 (26.7)	1815 (28.0)
<i>Trifolium pratense</i>	0	2 (3.4)	0	35 (1.1)	106 (9.7)	7 (2.8)	6105 (17.6)* ⁴	95 (1.5)* ⁴
<i>Erigeron annuus</i>	0	1 (1.7)	0	20 (0.6)	126 (11.5)	37 (14.6)	3705 (10.7)	1220 (18.8)
<i>Rudbeckia laciniata</i>	0	0	0	0	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0	58 (5.3)	0	3190 (9.2)* ³	0 (0.0)* ³
<i>Geum aleppicum</i>	7 (5.5)* ²	0 (0.0)* ²	875 (11.8)* ⁴	0 (0.0)* ⁴	45 (4.1)	7 (2.8)	825 (2.3)	255 (3.9)
<i>Phytolacca esculenta</i>	0	0	0	0	0	0	0	0
<i>Medicago sativa</i>	0	0	0	0	33 (3.0)	0	1090 (3.1)	0
<i>Stachys Riederi</i>	0	0	0	0	13 (1.2)	0	295 (0.9)	0
<i>Petasites japonicus</i>	4 (3.1)	2 (3.4)	1100 (14.9)	275 (8.3)	0	0	0	0
<i>Glechoma hederacea grandis</i>	10 (7.8)* ³	0 (0.0)* ³	180 (2.4)	0	0	0	0	0
Others	18 (14.1)	6 (10.2)	635 (8.6)	320 (9.7)	52 (4.7)* ³	43 (16.9)* ³	1010 (2.9)* ⁴	1440 (22.2)* ⁴
Total (other plants)	126 (98.4)	59 (100.0)	7365 (99.6)	3305 (100.0)	558 (50.8)	141 (55.5)	25455 (73.5)	4825 (74.3)
Grand total	128 (100.0)	59 (100.0)	7395 (100.0)	3305 (100.0)	1098 (100.0)	254 (100.0)	34635 (100.0)	6490 (100.0)
No. spp.	8		10 (1.9)		20		27 (6.7)	
Duration/visit			57.8 55.7				31.5 25.6	

Significantly different between sexes: *P<0.05; **P<0.02; ***P<0.01;

Percentage ratio is given in parentheses.

G ₂				Total						Duration/visit	
V		D		V (cases)			D (seconds)			(seconds)	
♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	Total	♀♀	♂♂	Total	♀♀	♂♂
603 (56.6)	621 (44.7)	5615 (22.3)	6000 (24.0)	939 (41.0)	658 (38.6)	1597 (40.0)	8420 (12.5)	6575 (18.9)	14995 (14.7)	9.0	10.0
25 (2.3)	0	360 (1.4)	0	192 (8.4)	54 (3.2)	246 (6.2)	5840 (8.9)*	765 (2.2)*	6605 (6.5)	30.4* ²	14.2* ²
21 (2.0)	1 (0.1)	315 (1.2)	5 (0.0)	59 (2.6)	22 (1.3)	81 (2.0)	1230 (1.8)	305 (0.9)	1535 (1.5)	20.8	13.9
9 (0.8)	0	95 (0.4)	0	9 (0.4)	1 (0.1)	10 (0.3)	95 (0.1)	25 (0.1)	120 (0.1)	10.5* ²	25.0* ²
0	0	0	0	1 (0.0)	0	1 (0.0)	10 (0.0)	0	10 (0.0)	10.0	—
658 (61.7)	622 (44.7)	6383 (25.3)	6005 (24.0)	1200 (52.4)	735 (43.2)	1935 (48.4)	15595 (23.2)	7670 (22.1)	23265 (22.8)	13.0	10.4
120 (11.3)	136 (9.8)	5890 (23.4)	4190 (16.8)	332 (14.5)	231 (13.6)	563 (14.1)	19700 (29.3)	8660 (24.9)	28360 (27.8)	59.3*	37.5*
135 (12.7)* ³	489 (35.2)* ³	5575 (22.1)	12000 (48.0)	241 (10.5)* ³	498 (29.2)* ³	739 (18.5)	11680 (17.4)* ²	12130 (34.9)* ²	23810 (23.3)	48.5* ³	24.4* ³
29 (2.7)	21 (1.5)	345 (1.4)	255 (1.0)	155 (6.8)	59 (3.5)	214 (5.4)	4050 (6.0)	1495 (4.3)	5545 (5.4)	26.1	25.3
105 (9.8)* ³	2 (0.1)* ³	6640 (26.3)* ⁴	25 (0.1)* ⁴	105 (4.6)*	2 (0.1)*	107 (2.7)	6640 (9.9)* ³	25 (0.1)* ³	6665 (6.5)	63.2* ³	12.5* ³
2 (0.2)	6 (0.4)	10 (0.0)	65 (0.3)	60 (2.6)	6 (0.4)	66 (1.7)	3200 (4.8)*	65 (0.2)*	3265 (3.2)	53.3* ⁴	10.8* ⁴
0	4 (0.3)	0	150 (0.6)	52 (3.3)	11 (0.6)	63 (1.7)	1700 (2.5)	405 (1.2)	2105 (2.1)	32.7	36.8
0	57 (4.1)	0 (0.0)* ²	1670 (6.7)* ²	0	57 (3.3)	57 (1.4)	0 (0.0)*	1670 (4.8)*	1670 (1.6)	—	29.3
0	1 (0.1)	0	20 (0.1)	33 (1.4)	1 (0.1)	34 (0.9)	1090 (1.6)	20 (0.1)	1110 (1.1)	33.0	20.0
10 (0.9)	33 (2.4)	285 (1.1)	520 (5.1)	23 (1.0)	33 (1.9)	56 (1.4)	580 (0.9)	520 (1.5)	1100 (1.1)	25.2	15.8
0	0	0	0	4 (0.2)	2 (0.1)	6 (0.6)	1100 (1.6)	275 (0.8)	1375 (1.3)	275.0* ⁴	137.5* ⁴
0	0	0	0	10 (0.4)	0	10 (0.3)	180 (0.3)	0	180 (0.2)	18.0	—
7 (0.7)	19 (1.4)	80 (0.3)	75 (0.3)	77 (3.4)	68 (4.0)	145 (3.6)	1725 (2.6)	1835 (5.3)	3560 (3.5)	22.4	27.0
408 (38.3)	768 (55.3)	18825 (74.7)	18970 (76.0)	1092 (47.6)	968 (56.8)	2060 (51.6)	51645 (76.8)	27100 (77.9)	78745 (77.2)	47.3*	28.0*
1066 (100.0)	1390 (100.0)	25210 (100.0)	24975 (100.0)	2292 (100.0)	1703 (100.0)	3995 (100.0)	67240 (100.0)	34770 (100.0)	102010 (100.0)	29.3	20.4
15	23	27 (10.1)		36	30	45	45 (5.5)				
		23.6	18.0				29.3	20.4	25.5		

**P<0.001

album, being scarce, was more frequently visited by $G_2 \sigma$ than $G_2 \varphi$, probably due to its coloration. In general for *Re*, males were attracted by whitish plants, while females by oviposition plants, probably due to their different urge.

This conclusion can be extended to dead plants, stones and soil. In spring the males ($G_h \sigma$) rested on the whitish dead plants (16.8%), whitish stores, broken pieces of chinas or glittering glass, and cans (33.6%), which were exposed when the plant cover was sparse. $G_{1,2} \sigma$ preferred most whitish leaves, and rarely rested on dead leaves and soil or stones (G_1 : 2.1%, 6.5%; G_2 : 0.3%, 5.3%). $G_h \varphi$ rested on stones and soil as much frequently (33.7%) as $G_h \sigma$, and $G_{1,2} \varphi$ also preferred stones and soil to rest (14.4%, 11.6%), because the summer females often visited farms and gardens for egg laying, where they had more chance to rest on soil and stones.

S-1: *Males tend to rest on whitish plants and objects, while females on oviposition plants.*

The sexual difference in preference of resting sites was also observed as to the plants which are neither whitish nor used for oviposition (3rd group in Table 3). It was partly attributed to the different height among these plant. The most contrasting case: *Helianthus tuberosus* (30–300 cm high) was more preferred by males than by females, while *Plantago asiatica* (5–50 cm high) vice versa. Even on oviposition plants, the highest species, *Armoracia rusticana* (60–130 cm in G_2) was more preferred for *resting* (*Re*) by males than by females. The sexual difference is exemplified in Table 4 by the record of 2 older individuals. In a single species, *C. album* var. *centrorubrum*, females rested on the lower part, while males on the upper part. We often observed a similar tendency in other adults.

S-2: *Males tend to rest on higher sites than females.*

As shown in Table 3 bottom, females used larger number of plant species as the resting site than males did (G_h : 26 vs 10; G_1 : 46 vs 30), but the difference became smaller toward autumn (G_2 : 35 vs 30). This may be caused by the sexual difference in resting habit for height and vegetation. In spring there were few tall species preferred by males. After many plants grew high in early autumn, however, females could use not only lower plants but also lower parts of tall plants.

A result supporting S-2 was obtain by YAMAMOTO (1983a) who measured the height above the ground on *resting* (*Re*), *flying* (*FL*) and *nectar intake* (*Ni*): 17.9cm (σ) – 8.1cm (φ) in *Re* ($p < 0.1$), 49.6 (σ) – 33.2 (φ) in *FL* ($p < 0.1$), 31.8 (σ) – 17.9 (φ) in *Ni* ($p < 0.05$), respectively.

2. Plants for nectar intake (Ni)

Table 5 presents the record of flower visit for *Ni*, separately for each sex and generation. Number of total visits (V) and total duration (D) of *Ni* were respectively compiled. Some nectar plants were significantly preferred by either females or males. Females: *Raphanus* (only in G_1 , V), *Rorippa*, *Rudbeckia*, *Trifolium repens*, *Geum* (only in G_h) and *Glechoma* (only in G_h , V); Males: *Trifolium pratense* (only in G_2 , V), *Phytolacca* and others (only in G_1). *Raphanus* and *Rorippa* are oviposition plants and

Phytolacca is a plant with whitish leaves. It probably relates to S-1. Plant heights of *Trifolium repens* is lower (10–30cm) than *T. pratense* (30–60cm). It may relate to S-2. However, neither S-1 nor S-2 can elucidate why *Rudbeckia*, *Medicago*, *Geum* and *Glechoma* were preferred by females rather than males.

The important nectar plants (V+D, ♂♂+♀♀) in each generation were transitional: *Taraxacum*, *Petasites* and *Geum* in G_h ; *Raphanus*, *Rorippa* and *Erigeron* in G_1 ; *Raphanus*, *Rudbeckia* and *Trifolium pratense* in G_2 .

The duration per flower visit was shorter in males than in females on 10 cases out of 14 (6 out of 10, significant in χ^2 -test; see the last column of Table 5). Its variance was significantly different from that in females (F-test, $p < 0.05$).

S-3: For nectar intake (N_i), females tend to stay for longer time on flowers than males.

OHSAKI (1979) reported 27 species as 'adult nectar plants' of *P. rapae crucivora* observed in Honshu (Aichi Pref.). In our result, a total of 45 plant species were recorded but the average number of plant species utilized by an individual was much smaller (Table 5). The difference between OHSAKI's and our result may depend upon the difference in census methods rather than in localities (cf. Introduction). Our result included more plant species sporadically visited than OHSAKI's. *Trifolium pratense* and *Erineron annuus* were 2 most important food sources as well as in OHSAKI's. Beside them *Taraxacum officinale*, *Raphanus raphanistrum* and *Rorippa sylvestris* were also important in Sapporo (Table 5).

3. Flying (FL)

The duration of FL includes *wandering flight* (W_f), *female-searching flight* (F_f) and *escaping flight* (E_f). Their flight pattern could not be easily distinguished during trailing.

The percentage frequency of time spent for FL is plotted in Fig. 2, to grasp a simple outline of its distribution pattern. The data from older individuals were omitted to avoid the influence by age (cf. next section). The distribution patterns shown by the 6 blocks in Fig. 2 were significantly different each other except G_h (a) – G_h (b) (either¹⁾ KOLMOGOROV-SMIRNOV 2-sample test or Two-sample median test). But the 3 distribution curves within a block were similar to each other except for b (G_h vs G_1 , G_2), d (G_h vs G_1 , G_2) and e (G_1 vs G_h , G_2) blocks (both²⁾ KOLMOGOROV-SMIRNOV 2-sample test and Two-sample median test).

Flying (FL) contained 2 main behavioral sequences: FL after *resting* ($Re \rightarrow FL$) and FL after *nectar intake* ($N_i \rightarrow FL$).

$Re \rightarrow FL$ (Fig. 2, left): Most FL of egg-laying females were *wandering flight* (W_f), which was used to move from one laying site to another, lasting over 10s (Fig. 2, a) as well as a searching behavior. FL of non-laying females consist of many short W_f (Fig. 2, b; except G_h discussed later). The frequency distribution in males (Fig. 2, c) was different from that in females. The percentage of 30s-or-more FL is very high.

¹⁾ Lenient criterion for difference.

²⁾ Severe criterion for similarity.

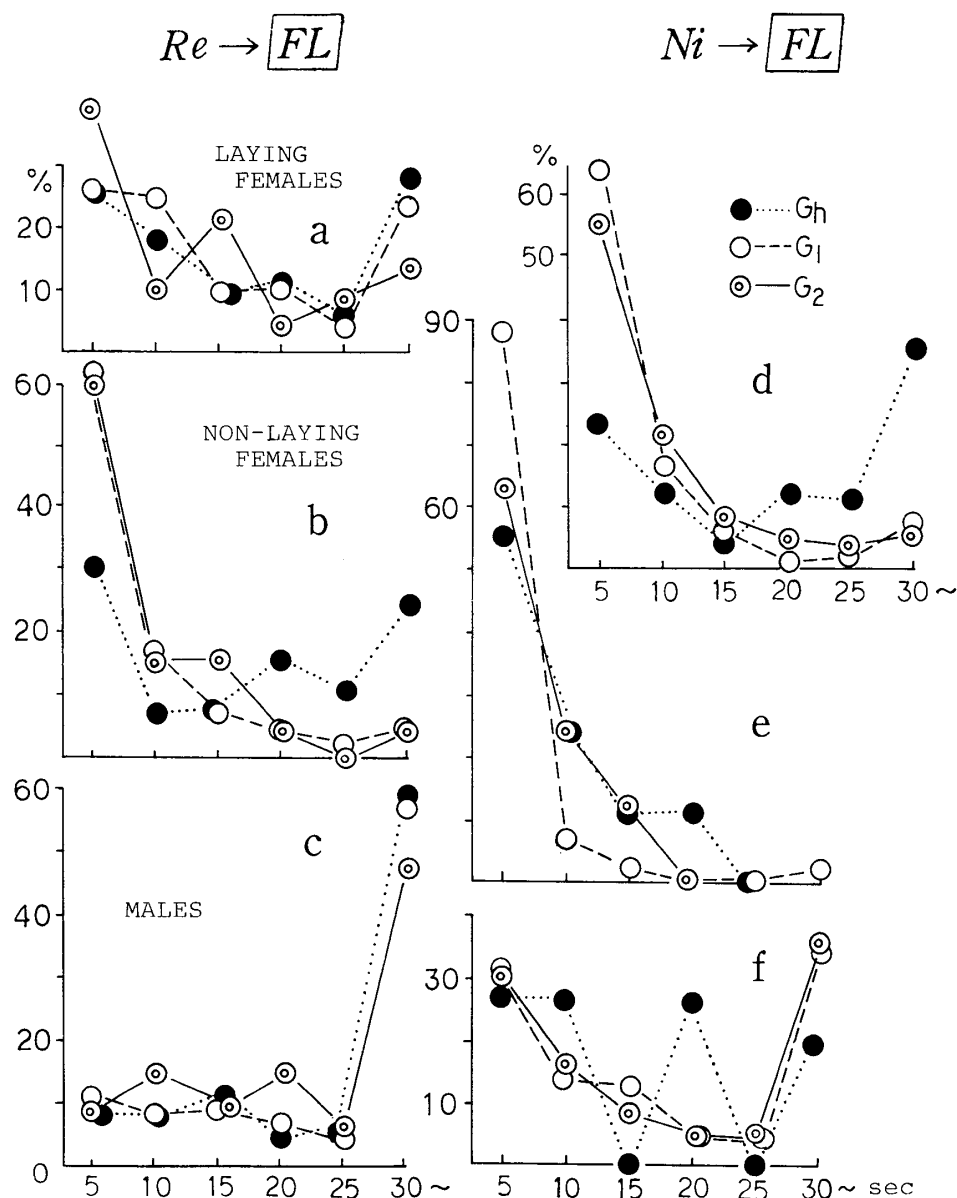


Fig. 2. The frequency distributions of time spent for *flying* (FL) after *resting* (Re) (a-c) or *nectar intake* (Ni) (d-f), based on the data of younger adults: laying females (a and d), non-laying females (b and e) and males (c and f). The difference was significant by KOLMOGOROV-SMIRNOV 2-sample test and Two-sample median test (ISHII, 1975) except for a part of b, d and e.

It suggests that most FL of males are *female-searching flight* (Ff), because we often observed that the duration of Wf was almost within 5 s, whereas that of Ff is variable, mostly over 10 s.

Ni → FL (Fig. 2, right): Short Wf is plausible because of short distance from flower to flower. Accordingly, the frequency distribution in *Ni* → FL transition skews to the shorter side than in *Re* → FL.

The difference in FL-duration among generations was obscure in males, but in egg-laying females the duration tended to skew to the longer side in G_h than $G_{1,2}$. This

probably relates to the scarcity of flowers for *nectar intake* (Ni), and of plants for egg laying. It may depend on the appetite behavior governed by hunger urge and egg-laying one. An unsatisfying appetite behavior will result in a long flight.

The longer-side skewing in G_h (cf. Fig. 2, b, d) is related to MIYAKAWA's study. MIYAKAWA (1976) found that *P. rapae crucivora* preferred grassland to bare ground. Accordingly, the butterflies in G_h must navigate among 'islands' of grasses or flowers in the sparse plant cover in early spring.

S-4: *The durations of flying (FL) are significantly different between egg-laying females, non-laying ones, and males.*

Actively flying males were attracted by various whitish objects, and often made contact with them. The most attractive object (11 out of 50 cases) was the cocoons of *Apanteles glomeratus*, the parasitoid wasps of *Pieris*, being probably caused by their mere abundance. The following items are whitish objects that attracted males: Dead leaves of *Chenopodium* and *Artemisia* (6 cases), pieces of white pottery (4), fuzzes of dandelion (4), onion heads (4), egg chambers of clubionid spiders (3), undersides of *Chenopodium* and wheat (3), white cocoon of a small moth (1), white flower of Common Bind Weed (2), white cap of a bottle (1), white feather of a bird (1), and stub of grass (1). OBARA and HIDAKA (1964) also reported that flying males approached to and contacted with whitish objects. These flying habits of males may increase the chance of resting on whitish objects (cf. S-1).

S-5: *Flying males are attracted by any whitish objects.*

4. Age-linked difference in interindividual behaviors

Relative frequencies of 3 patterns in *chasing gyration* (CG), i.e. *chasing* ($Ch/$), *being chased* ($/Ch$) and *gyrating* (Gy), varied with age in both sexes of $G_{1,2}$ (Table 6). Observed cases of interindividual behaviors in G_h were so few (cf. Table 9 and 10) that the data of G_h were omitted in this section. Males and younger females showed higher frequencies of $Ch/$ and Gy ; especially males were apt to chase eagerly other individuals, whereas older females were more passive (significant only in $/Ch$). For example, younger males ($\sigma 12$ and $\sigma 27$) very frequently gyrated with other younger males, and sometimes chased females and older males, whereas some older females (e.g. $\sigma 47$) were frequently chased by or occasionally responded with Gy to others.

The clear sexual difference was found in the relative frequencies of CG (Table 6; left). In older females: the order is $Ch/ < Gy < /Ch$ (9.0 – 24.4 – 66.7%, χ^2 -test, $p < 0.001$); in younger males: $/Ch < Ch/ < Gy$ (7.9 – 12.0 – 80.2%, $p < 0.001$). The former might mean a passive female-life (the frequency of *being chased* ($/Ch$) is the highest), while the latter an active male-life. On the other hand, the order ($Ch/ < /Ch < Gy$) was similar between younger females (20.2 – 31.5 – 48.3%, $p < 0.01$) and older males (9.5 – 27.6 – 62.9%, $p < 0.001$). This may relate to a stronger flight power of younger individuals than older ones.

There were also some age-linked differences in responses of non-flying individuals (Table 6, right). In the relative frequency, the older males were less active than the youngsters. Frequent *fluttering* (Ft) in the older males means that they oftener rested

Table 6. Frequency of interindividual behaviors by younger and older individuals in G_1 and G_2 . *Ch*: Chasing. *Ch*: Being chased. *Gy*: *Gyrating*. *Af*: *Ascending fight*. *To*: *Taking-off*. *Le*: *Leaning*. *Ae*: *Abdomen erecting*. *Wd*: *Wing folding*. *Ft*: *Fluttering*. *Ft*: *Being fluttered*. *Ae*: *Being responded with Ae*.

Individual code	Age in days	<i>Ch</i> /	<i>/Ch</i>	<i>Gy</i>	Total	<i>Af</i>	<i>To</i>	<i>Le</i>	<i>Ae</i>	<i>Wd</i>	Total
♀5	3-5	5	4	9	18	1	11	7	3	11	32
♀10	1-3	4	1	4	9	2	12	34	10	5	61
♀17	2-4, 5-7	2	3	11	16	2	23	152	20	31	226
♀22	2-3	1	1	1	3	0	2	3	0	4	9
♀26	4-5	5	10	12	27	3	35	54	35	8	132
♀41	1-2	1	9	6	16	1	20	25	28	1	74
Total (younger) % (a)	1-7	18 20.2	28 31.5	43 48.3	89 100.0	9 —	103 19.3	275 51.5	96 18.0	60 11.2	534 100.0
♀23	7-8	6	25	4	35	0	3	3	11	3	20
♀47	10-19	1	27	15	43	0	24	137	101	37	299
Total (older) % (b)	7-19	7 9.0	52 66.7	19 24.4	78 100.0	0 —	27 8.5	140 43.9	112 35.1	40 12.5	319 100.0
Significant difference between (a) and (b)	($p \chi^2 < \cdot$)	0.05	0.001	0.01			0.05	0.5	0.02	0.8	
♂7	4	6	3	126	135	1	0	0	2	0	2
♂12	2-4	21	22	143	186	1	51	16	1	6	74
♂24	1-3	2	0	11	13	0	11	12	0	1	35
♂27	3-6	76	44	424	544	2	65	20	35	17	145
Total (younger) % (c)	1-6	105 12.0	69 7.9	704 80.2	878 100.0	4 —	127 49.6	48 18.8	36 14.1	26 10.2	256 100.0
♂11	15, 16	13	8	22	43	1	6	14	5	2	29
♂29b	18-20	6	56	124	186	0	19	7	9	3	38
♂45	8, 21-23	18	44	100	162	0	22	25	1	1	49
Total (older) % (d)	8-23	37 9.5	108 27.6	246 62.9	391 100.0	1 —	47 40.5	46 39.7	15 12.9	6 5.2	116 100.0
Significant difference between (c) and (d)	($p \chi^2 < \cdot$)	0.7	0.001	0.2			0.5	0.01	0.9	0.3	0.1

than the younger males. In older females the observed frequency of *taking-off* (*To*) was lower, and that of *abdomen erecting* (*Ae*) higher than in younger females. Generally, older individuals became more passive (or more sedentary) than the youngsters.

S-6: *Older individuals are more sedentary than younger ones. Especially, older females more frequently exhibit abdomen erecting (Ae) than the youngsters.*

Ascending flight (*Af*) were observed almost exclusively in younger individuals (13/14, Table 6) in $G_{1,2}$. The average age of the individuals which performed *Af* was 3.6 days (Table 7).

SHAPIRO (1970) reported *Af* of *Pieris* females as 'ascending male-avoidance flight'. Similar function, to curtail male courtship attempts, was suggested in *Colias* (RUTOWSKI, 1978) and in *Agapetes* butterflies (SONNTAG, 1981). In our observations, females took *Af* after *abdomen erecting* (*Ae*) in 7 cases (♀10h, ♀22, ♀10, ♀17 and ♀26, Table 7), suggesting a male-avoidance function. And we observed 2 cases that a male (♂12h or ♂12) performed *Af* like as a female after being chased by another male. Consequently, *Af* may be regarded as a kind of *escaping flight* (*Ef*). Moreover, ♂27 was chased by a dragonfly and ascended about 5 m high above the ground.

SHAPIRO (1970) studied populations of *Pieris protodice* and suggested that a frequent sexual interaction in a dense population made a mated female emigrate from home habitats and colonize in new habitats. In our *P. rapae crucivora*, we sometimes (4/11) missed a marked female after *Af* (Table 7), because the female continued to ascend even after the male returning. The behavioral sequence before *Af* (Table 7) shows that *Af* is related to *chasing* (*Ch*/) or *being chased* (/ *Ch*) (12 out of 19 cases). Not older females but younger ones avoided males with *Af*. Furthermore, according to OHSAKI (1980), younger females show a migratory flight, and reproductive females and all males are strongly resident within suitable habitats. Similar result was got in our study. YAMAMOTO (1981a) already reported that the duration of stay in home habitat was longer in males than in females. The average duration of stay within concentric circles (100 to 900 m in diameter) from the releasing point were 3.1 days (100m) – 6.5 (900m) (G_h ♂), 6.0 – 7.3 (G_1 ♂), 14.0 – 16.3 (G_2 ♂), 2.8 – 4.8 (G_h ♀), 3.0 – 4.1 (G_1 ♀) and 4.4 – 6.2 (G_2 ♀). Consequently, it is suggested that younger females tend to emigrate from home habitats.

YAMAMOTO (1983b) studied the relationship between sex ratio and flight activity in *P. rapae crucivora*, comparing with *P. napi nesis*, which adopts no *Af* as male-avoidance behavior. The former showed more male-biased sex ratio and earlier emigration of young females than the latter species.

S-7: *Ascending flight (Af) is found between younger individuals, which probably results in emigration of younger females from home habitats. Younger females, which exhibit more Af than older ones, may be expelled by sedentary males out of home habitats.*

5. Sexual and seasonal differences in interindividual behaviors

Most resting females responded with *leaning* (*Le*) to the approaching conspecific

Table 7. The situations before and after *ascending flight* (*Af*). The parenthetical numbers denote the duration (seconds) of the respective behavior pattern.

Individual code	Age in days	Date	Time	Behavioral sequence
♂12h	2	May 11	10:11	♂/Ch → Af(60) → Ni (Ni: nectar intake)
♂16	6	24	11:30	Ch/♀ → Af(15) → FL (FL: flying)
♂7	4	Jul. 4	10:05	Ch/♀ → Af(15) → FL (Ch/: chasing)
♂12	2	9	08:19	♂/Ch → Af(20) → FL (/Ch: being chased)
♂11	16	21	16:54	Ch/♀ → Af(55) → FL
♂27	5	Aug. 3	12:17	Ch/♀ ⁿ → Af(20) → FL (♀ ⁿ : a female of <i>Pieris napi nesis</i>)
	6	4	08:22	Ch/♀ → Af(8) → FL
Mean (males)	5.9 (3.6) ^a		11:03 (10:07) ^a	
♀10h	2	May 10	12:37	Re → To → ♂/Ch → Ae → Af → oversighted (To: taking-off)
♀22	4	30	10:37	Re → Ae(2) → To → Af(8) → Ni (Ae: abdomen erecting)
♀5	4	Jul. 2	10:14	Ni → To → FL(5) → ♂/Ch → Af(15) → Ni (Re: resting)
♀10	3	8	12:03	Re → FL(10) → ♂/Ch → Af(25) → FL (Sw: swarming)
			12:58	Ae(45) → Af(55) → oversighted (El: egg laying)
♀17	3	13	10:07	Ni → Ae(5) → To → Sw(5) → Af(20) → El
	6	17	12:23	El → ♂/Ch(5) → Af(10) → ♂/Ch(5) → Af(10) → ♂/Ch → FL
♀26	4	29	11:18	Ni → Ae(50) → To → Af(20) → FL(20) → Ni
			11:40	Ni → Ae(20) → To → Af(70) → oversighted ^b
♀41	5	30	15:17	Ni → Ae(10) → To → FL(5) → Ae(15) → To → Af(25) → Fl(30) → Ni
	2	Aug. 7	15:12	El → ♂/Ch → Af(45) → FL → oversighted
Mean (females)	3.6		12:10	

^aExcluding ♂11, exceptionally old.^bDiscovered after 5 min.

Table 8. Responses of ♀47 to approaching butterflies and cars at various distances. Incomplete or weak responses in parenthesis.

Response	Approaching objects	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	90	100	110	120	130	140	150	Median	Two-sample median test
<i>Wing folding</i> (<i>Wd</i>)	<i>P.r.c.</i> ♂					2		1	3	2	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	60.0 (55.0)	n.s.
	cars							(1)	(3)	(3)	(1)	(1)	(1)	(1)	(1)										1 (1)	n.s.	n.s.
<i>Leaning</i> (<i>Le</i>)	<i>P.r.c.</i> ♂	1				6	3	25	25	27	7	3	12	2	2	8	1	9	3							47.2 (50.0)	n.s.
	<i>P.r.c.</i> ♀							(1)	(1)	(2)																n.s.	n.s.
	<i>F.a.p.</i>								1	(1)																n.s.	n.s.
<i>Twitching</i>	<i>P.r.c.</i> ♂						1	4	3	1																	
No response	<i>P.r.c.</i> ♂		1	1		4		9	8	11	3	3	4	6	6	1	2	1								47.9	*
	<i>C.e.p.</i> ♂			1									1														*
<i>Abdomen erecting</i> (<i>Ae</i>)	<i>P.r.c.</i> ♂	10	12	7	3	1	1																			5.4 (19.3)	*
	<i>C.e.p.</i> ♂				(4)	(3)	(13)	(1)	(3)	(2)																	
	<i>C.e.p.</i> ♀										(1)																

P.r.c. : *Pieris rapae crucivora*. *C.e.p.* : *Colias erate poliographus*. *F.a.p.* : *Fabriciana adippe pallescens* (Nymphalidae).

* $p < 0.001$. n.s. : not significant.

Table 9. The total cases of the of responses by a feeding or resting individual to an approaching object. The corrected number is given in parentheses for comparing with the case of G_h (divided by the relative duration of observed seconds). The cases on older adults were omitted.

Response (a-d) or Approaching objects (f-l)	Non-flying females			Response	Non-flying males		
	G_h	G_i	G_s		G_h	G_i	G_s
a. <i>Wing folding</i> (Wd) %	1 5.3	<<< 16.5	>>> 6 (8)	Wd %	0 0.0	10 (3) 7.4	3 (2) 3.9
b. <i>Abdomen erecting</i> (Ae) %	7 36.8	< >>>	>> <<<	b'. /Ae ¹ %	2 10.0	15 (5) 11.1	8 (5) 10.5
c. <i>Leaning</i> (Le) %	3 15.8	<<< 52.1	= 39.7	c'. Ft ² %	10 50.0	33 (11) 24.4	20 (13) 26.3
d. <i>Taking-off</i> (To) %	8 42.1	<<< >	= 25.0	To %	8 40.0	77 (25) 57.0	45 (28) 59.2
e. Total (a-d or f-l) %	19 100.0	<<< 100.0	< 100.0		20 100.0	135 (44) 100.0	76 (48) 100.0
f. <i>P. rapae crucivora</i> ♂ %	12 63.2	<<< 75.2	<< 81.4		13 65.0	85 (28) 63.0	47 (29) 61.8
g. <i>P. rapae crucivora</i> ♀ %	2 10.5	> 1.9	> 0.0		2 10.0	16 (5) 11.9	8 (5) 10.5
h. <i>P. napi nesis</i> %	4 21.1	= >>>	= 0.0		4 20.0	11 (4) 8.1	0 0.0
i. <i>Colias erate poligraphus</i> %	1 5.3	<<< 8.5	= 10.3		0 0.0	3 (1) 2.2	10 (6) 13.2
j. Other butterflies %	0 0.0	= 1.4	= 0.0		1 5.0	4 (1) 3.0	0 0.0
k. Other insects %	0 0.0	= 1.4	= 1.0		0 0.0	8 (3) 5.9	11 (7) 14.5
l. Others %	0 0.0	<<< 11.0	= 7.3		0 0.0	8 (3) 5.9	0 0.0
m. Observed duration (s) ratio	132,170 1.00	230,525 1.74	104,105 0.79		29,415 1.00	90,440 3.07	47,115 1.60
n. Total (s) [ratio]		466,800	[2.80]			166,970	[1.00]
o. Case / h	0.54	<	7.05		2.45	5.74	5.81

χ^2 -test: “=”: $0.2 < P$; “ \leq ”: $P < 0.2$; “<”: $P < 0.05$; “ \ll ”: $P < 0.01$; “ $\ll\ll$ ”: $P < 0.001$

¹ When an approaching female found a non-flying male, she responded with Ae for herself.

² *Fluttering*

adults, other butterflies, other insects in flight, and even any moving objects, *e.g.* a thrown stone and a fluttered insect-net (observed in ♀10, Aug. 7) but *Le* was released most easily and strongly by the conspecific males approaching within a range of 30–50 cm (*cf.* Table 8).

From our observations of marked females, we got the following generalization: A resting female with her wings opened first exhibits *wing folding* (*Wd*) to a male approaching at 20–150 cm distant before *Le*. But *Le* sometimes appears on the way of *Wd* by a sudden appearance of a male within 45 cm. On the other hand, *abdomen erecting* (*Ae*), the posture being contrary to *Wd*, is the reaction to males approaching within 20 cm (*cf.* Table 8).

Weak *leaning* (*Le*), twitching of wings or body and no response were often observed when males were at 20–100 cm distant, and probably caused by the reciprocal prevention of the different movements between *Wd* and *Le* which have the equal values of the median in the distance of approaching males (Table 8, last 2 column). As *Ae* have different medians from *Wd* and *Le* (5.4 cm, 60.0, 47.2), the median of incomplete *Ae* (19.3 cm) suggests the prevention by *Wd* or *Le*.

A confused case was observed: In ♀10 on July 8, *Ae* was first released as a response to the sudden appearance of a male at a close distance, then successively followed by *Wd* and *Le* after the male flew away.

S-8: A female responds with wing folding (*Wd*) or leaning (*Le*) to a male approaching at 20–150 cm distant whether or not the male is aware of her, and with abdomen erecting (*Ae*) to a male perceiving and approaching her within 25 cm distant.

Non-flying younger individuals (Table 9) or flying younger ones (Table 10) interacted with conspecific ones, different butterfly species, other insects and moving objects (men, cars, grasses, *etc.*). The data of older individuals were omitted, because they are few.

Adult butterflies of G_h appear from late April on the study area, and reach a peak in number in late May or early June. The population density per day in G_1 (early July) increases over twice as many as G_h , then that in G_2 (mid August) decreases slightly, *i. e.* $G_h \lll G_1 \geq G_2$ ($p < 0.001$ at the peak between G_h and G_1 , $p < 0.1$ between G_1 and G_2 , *cf.* YAMAMOTO and OHTANI, 1979). If each of interindividual behaviors is based on a random encounter, the seasonal change of its frequency would become parallel with the above order. However, non-parallel cases are found in Tables 9 and 10: Non-flying females most frequently exhibited *Ae* in G_2 of 3 generations (Table 9, b), and they were most frequently approached by males in G_2 (f); Flying females were most frequently chased by males in G_2 (Table 10, b, h), flying males happened to meet *Colias* most frequently in G_2 (k) (These are probably caused by the sedentariness in G_2 -males); Flying males were fluttered more frequently by resting males in G_h (Table 10, f) (this is probably caused by the poor growth of vegetation in G_h); Both sexes happened to meet *P. napi nesis* most frequently in G_h (Tables 9, h and 10, j) (this may be related to the decrease of clear habitat segregation between *P. rapae* and *P. napi*, which is caused by the poor vegetation in G_h).

Some resting males responded to approaching objects with *Ft*, not with *Le* as in

Table 10. The total cases of the number of interindividual events observed in a flying individual pursued. The number in parentheses is corrected by observation time for comparing with the number of G_h . The cases on older individuals were omitted.

Events (a-f) or Encountered butterflies (h-l)	Flying females			Flying males		
	G_h	G_i	G_2	G_h	G_i	G_2
a. Chasing (Ch/) %	2	10 (18)	6 (13)	3	35 (24)	76 (25)
b. Being chased (Ch) %	12.5	21.3	13.3	3.7	11.0	13.2
c. Gyration (Gy) %	6	9 (16)	19 (40)	2	25 (17)	44 (14)
d. Swarming (Sw) %	37.5	19.1	42.2	2.4	7.8	7.8
e. Ascending flight (Af) %	4	21 (38)	16 (33)	59	250 (175)	424 (139)
f. Being fluttered (Ft) ¹ %	25.0	44.7	35.6	72.0	78.4	73.8
	2	1 (2)	0	0	4 (3)	3 (1)
	12.5	2.1	0.0	0.0	1.3	0.5
	12.5	6 (11)	4 (8)	2	2 (1)	2 (1)
	—	12.8	8.9	2.4	0.6	0.3
	—	—	—	16	3 (2)	25 (8)
	—	—	—	19.5	0.9	4.4
g. Total (a-f or h-l) %	16	47 (84)	45 (94)	82	319 (223)	574 (188)
	100.0	100.0	100.0	100.0	100.0	100.0
h. <i>P. rapae crucivora</i> ♂	5	32 (57)	40 (83)	50	291 (203)	462 (151)
i. <i>P. rapae crucivora</i> ♀	31.3	68.1	88.9	61.0	91.2	80.5
j. <i>P. napi nesis</i>	5	6 (11)	3 (6)	2	24 (17)	11 (4)
k. <i>Colias erate poligraphus</i>	31.3	12.8	6.7	2.4	7.5	1.9
l. Other butterflies	4	1 (2)	0	24	4 (3)	2 (1)
	25.0	2.1	0.0	29.3	1.3	0.3
	12.5	2 (4)	2 (4)	5	0	94 (31)
	0	4.3	4.4	6.1	0.0	16.4
	0.0	5 (9)	0	1	0	5 (2)
	0.0	10.6	0.0	1.2	0.0	0.9
m. Observed duration (s) ratio	15,610	8,670	7,495	21,585	30,940	66,120
n. Total [ratio]	1.00	0.56	0.48	1.00	1.43	3.06
o. Case / h	3.69	31,775	[1.00]	13.65	118,645	[3.73]
		19.52	21.61		37.12	31.25

χ^2 -test: “=”: $0.2 < p$; “≤”: $p < 0.2$; “<”: $p < 0.05$; “≪”: $p < 0.01$; “≪≪”: $p < 0.001$

¹A resting male fluttered his wings to the flying male pursued.

females. The relative frequency of *Ft* was highest in G_h (Table 9, c'), probably related to the scarcity of roosting sites in spring. An male in *roosting flight* (*Rf*) sometimes released *Ft* of roosting males nearby.

The total observation time of interindividual behaviors in non-flying females is 2.80 times as much as that in non-flying males (Table 9, n), while that in flying males 3.73 times as much as that in flying females (Table 10, n). Grand total is 498,575 s (females) and 285,615 s (males), 1.75 : 1.00. Accordingly, the relative frequency of interindividual behaviors must be standardized by the observation time. It was 397 (694/1.75) in females, and 1,206 in males. Generally, males are more active than females, and interact with other individuals about 4 times as much as females do.

S-9: *The frequency of interactions among males is significantly higher than that among females in every generation. This difference is due to higher activity of flying males. The order of the frequency of every behavior involved in the interactions does not always coincide with order of the population density ($G_h \lll G_1 \geq G_2$), possibly caused by behavioral difference in males between G_1 and G_2 .*

6. Mating behavior and the activity of males

The copulation was observed 10 times in 1976 (Table 11). The average duration was 5,090 s, except for 2 very short cases ($\varnothing 2$: 1,220 s, $\varnothing 10$ h: 2,680 s). These 2 cases may mean an incomplete mating, as the partner males chased $\varnothing 2$ and a female of *P. napi nesis*, respectively, just after the end of copulation.

SUZUKI (1976b) reported multiple mating of *P. rapae crucivora* and estimated the average number at 2.84 times per female. We observed $\varnothing 13$ which mated after laying about 100 eggs. At 9:46 on May 15, $\varnothing 13$ in *resting* (*Re*) did not refuse *mating* (*Mt*) with a male. Seemingly, she failed to exhibit *abdomen erecting* (*Ae*) by his sudden approach. After this mating, $\varnothing 13$ continued *hanging* (*Ha*) for 5,080 s. Possibly, this was a case of multiple mating, though there was a doubt that $\varnothing 13$ was a virgin and laid unfertilized eggs.

In a dragonfly, *Sympetrum parvulum*, UÉDA (1979) reported the prolonged copulation time due to the interference by males in a dense population. In our butterfly, too, the interference by males seemed to lengthen the copulation time (Table 11). We also observed an abnormally long copulation lasting over 6 h (July 9). This pair was unable to detach even after being captured.

Therefrom, we observed additional 21 cases of *Mt* at the campus of Hokkaido University, Sapporo, in 1980 and at the field in Tabira-chô, Nagasaki Pref., northern Kyushu in 1981 (cf. Table 11). Judging from correlation coefficients between copulation time and interferences by males (bottom of Table 11), *fluttering* (*Ft*) of males to approaching males causes the prolonged copulation ($r=0.9055$, $p<0.01$). Further examination of the data, very low value of correlation coefficient is showed in the number of *Ft* under 25 ($r=0.2825$, $0.1<p$). This suggests a function of the driving-away in *Ft* (cf. OHTANI and YAMAMOTO, 1980). Too much frequent *Ft*, which is caused by the interference in a dense population, however, prevent the copulation from completion. When *Ft* was counted up to 207 times, the copulation time was prolonged up to 7.4 h (Table 11).

Table 11. The records of the mating of *Pieris rapae crucivora* in 1976, 1980 and 1981. Those in 1980 were collected at the same campus of Hokkaido University (Sapporo) as in 1976. The data in 1981 was at Tabira-chô (Nagasaki Pref.) in northern Kyushu. Pf: *Prenuptial flight*. DC: Duration of copulation. Nft: The number of flutter response by the mating male. Nbf: The number of taking-off by the mating pair. Dbf: Total duration of *Pair-bond flight* (bf).

Individual code	Age in days	Date	Time (start)	Pf-type ¹ -(duration, s)	DC (s)	Interference during copulation		
						Nft	Nbf	Dbf (s)
♀2	8	Apr. 26	11:14	1-(35)	1,220	0	0	0
♀10h	1	May 9	13:58	2-(20)	2,680	0	0	0
♀13	4	May 15	9:46	omitted	5,385	*	*	*
♀3	3	Jun. 25	12:10	2-(120)	5,435	1	5	35
♀4	2	Jun. 30	13:32	2-(15)	unsuccessful	—	—	—
			13:32	2-(5)	4,290	1	2	60
♀5	3	Jul. 1	7:54	1-(30)	5,250	*	*	*
♀10	1	Jul. 6	12:50	2-(15)	unsuccessful	—	—	—
			13:02	2-(30)	unsuccessful	—	—	—
	2	Jul. 7	9:52	2-(25)	unsuccessful	—	—	—
			9:53	2-(15)	3,510	*	*	*
♀7	2	Jul. 12	9:25	*	5,725	*	*	*
♀26	4	Jul. 29	8:30	*	*	*	*	*
♀41	1	Aug. 6	8:12	omitted	5,570	6	3	40
Correlation coefficient with DC (1976)						.6631	.8882	.7727
(statistical significance)						(nothing)	(p<.05)	(nothing)
♀2-80	4	Jul. 7	10:03	*	10,147	32	17	230
♀4-80	3	Jul. 7	10:35	2-(15)	5,925	20	4	45
♀7-80	2	Jul. 8	10:06	omitted	4,750	5	1	5
♀8-80	3	Jul. 8	10:10	1-(40)	3,490	19	5	45
♀17-80	1	Jul. 12	10:53	omitted ²	7,250	15	1	70
♀18-80	1	Jul. 13	14:08	omitted ³	4,825	6	3	20
♀19-80	2	Jul. 14	14:02	2-(59)	unsuccessful	—	—	—
			14:05	2-(120)	unsuccessful	—	—	—
♀20-80	2	Jul. 14	13:06	2-(2)	5,500	58	1	5
♀21-80	2	Jul. 15	9:43	omitted	5,145	17	2	50
♀22-80	3	Jul. 15	9:59	*	15,820	163	23	230
♀23-80	3	Jul. 16	13:36	1-(30)	3,650	15	4	50
♀24-80	2	Jul. 15	9:41	1-(40)	4,630	13	5	70
♀26-80	4	Jul. 16	13:28	omitted	6,235	7	3	40
♀28-80	1	Aug.26	13:27	*	5,610	19	4	65
Correlation coefficient with DC (1980)						.8575	.8819	.8642
(statistical significance)						(p<.001)	(p<.001)	(p<.001)
♀1-81	2	May 29	10:14	1-(10)	4,440	10	2	10
♀5-81	2	May 31	9:29	omitted ²	26,760	207	8	80
♀6-81	2	May 31	13:37	omitted	11,640	97	1	5
♀nn-81	*	Jun. 1	16:15	*	5,340	3	1	10
♀10-81	2	Jun. 2	9:29	omitted ²	4,290	25	0	0
♀11-81	2	Jun. 3	11:38	1-(5)	6,840	96	2	10
Correlation coefficient with DC (1981)						.9348	.9210	.9388
(statistical significance)						(p<.01)	(p<.01)	(p<.01)
Correlation coefficient with DC (all)						.9055	.5470	.4832
(statistical significance)						(p<.001)	(p<.01)	(p<.05)

*No observation.

¹Type-1 and Type-2 was distinguished by OHTANI (1985).

²*Abdomen erecting* (Ae) is exhibited incompletely.

³The failed down from the plant.

As the all partner males in Table 11 were unmarked individuals, their age and mating experience are unknown. According to OBARA (1983), there is a possibility that the age and multiple mating in males make the copulation time prolong. This will be remarked in further investigations.

Abdomen erecting (*Ae*) of a female prevents a male from *catching wings* (*cw*), that is, a male cannot catch the costae of her fore wings widely opened. To test whether the peculiar posture of *Ae* prevents not only *cw* but also other subsequent stages, fore wings of a mated female were stucked closely with adhesive tape. The erection of the abdomen prevented *grasping genitalia* (*gg*). *Ae* was able to prevent at least 2 stages of *Mt* sequence.

S-10: *Prolonged copulation is caused by the eager attempt of flying other males, but before it becomes more severe in a higher population density, fluttering* (*Ft*) of a male in copula is effective for driving an approaching male away.

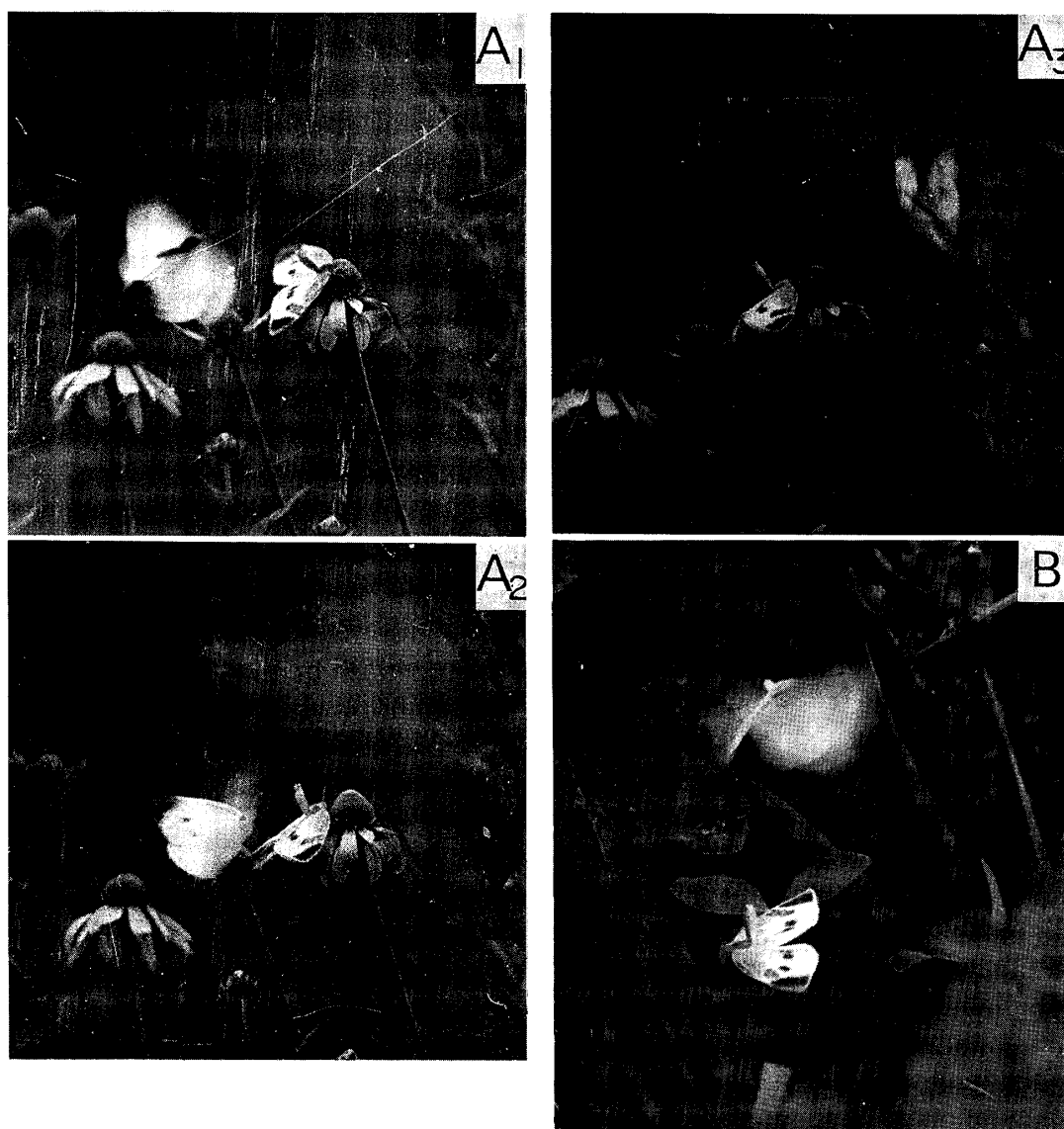


Fig. 3. 'Hovering' behavior of a male and *abdomen erecting* (*Ae*) of a female. A. ♀41 and an approaching male. Three shots were taken successively every 10 s; B. ♀47 and a hovering male.

SUZUKI *et al.* (1977) reported 'hovering' of *Pieris melete* females and 'caressing' of *P. canidia* males respectively as a species-specific pattern of courtship behavior. Further, SUZUKI (1979a) observed, though rarely, the 'hovering' also in *P. napi japonica*. In our *P. rapae crucivora*, too, the patterns similar to 'hovering' and 'caressing' were observed in 4 and 2 cases respectively. The available records are not yet sufficient, but they are cited below for further advance on the studies of the courtship behavior in various species and of the relation between caressing or hovering and mating eagerness of males at various population densities.

August 7, 1976 [12:15] : ♀41 in *nectar intake* (Ni) exhibited *abdomen erecting* (Ae) to an approaching male. This male initially stayed in the air at *ca.* 10 cm high above and behind ♀41 (Fig. 3, A₁). Thereafter, he approached slowly (Fig. 3, A₂), made a several faint contact with ♀41, then abruptly parted from her, flew around at 10–20 cm above and before her (Fig. 3 A₃) and flew away. The whole process took 45 s.

August 25, 1976 [15:33] : ♀47 in *resting* (Re) exhibited Ae to a male who approached at *ca.* 10 cm distant from her. The male parted from her and stayed at *ca.* 30 cm above her (Fig. 3, B). After 45 s the male tried to mate with her 3 times during 30 s, they flew away. [15:54] : Ae of ♀47 was also observed at the approach of another male, who flew around at *ca.* 10 cm above and behind her for 35 s soon as ♀47 ceased Ae, the male tried to touch her, which caused Ae again. After *ca.* 20 s, the male exhibited *swarming* (Sw) with other 2 males approaching nearby.

August 27, 1976 [13:14] : ♂45 chased a flying female, and she landed and exhibited Ae. ♂45 continued hovering at *ca.* 10 cm above the female for 30 s, and furthermore for 20 s after a trial of copulation. Thereafter, as the female took off abruptly, ♂45 ceased hovering to chase her.

Two cases of 'caressing' behavior were found in Ae of virgin females.

July 14, 1975 [13:15] : During a virgin female exhibited Ae for *ca.* 30 s, a male did not leave beyond 10 cm from the female and briefly touched her on the wings and the erected abdomen. Thereafter, the female folded her wings, but the male flew away.

August 6, 1976 [8:41] : ♀41 rested on the leaf after being marked at 7:36 and often exhibited *leaning* (Le). She exhibited *abdomen erecting* (Ae) to a male approaching within 10 cm of her. The male repeated to touch and fly around her within a range of *ca.* 10 cm for 80 s, during which she kept Ae. As soon as ♀41 folded her wings after the male flew away, a new male appeared, landed beside her and succeeded to mate with her.

7. Egg laying (El) and its pattern in each generation

Egg laying (El) were observed in 17 females on 7 cruciferous species, *Rorippa sylvestris*, *Ro. islandica*, *Sisymbrium officinale*, *Brassica campestris Napus*, *Raphanus raphanistrum*, *Ra. sativus* and *Armoracia rusticana*. OHSAKI (1979) reported 7 crucifers for *P. rapae crucivora* in Honshu, northern area of Aichi Pref. The plant species in common to the 2 areas are 2 cultivated crucifers, *B.c. Napus* and *Ra. sativus*. At our Campus field, 83.9% (1,613/1,922) of the observed eggs were laid on *Ro. sylvestris*. The

Table 12. The records of egg-laying patterns in 3 generations (G_n , G_1 and G_2). A : Average number of eggs laid per hour. B : Average duration for an egg laying (El). C : Number of El per hour. D : Average number of eggs laid per El . E : Number of empty oviposition per hour. CC : Correlation coefficient.

Individual code	A (eggs)	B (s)	C (cases)	Number of eggs laid per El							D (eggs)	E (cases)
				1	2	3	4	5	6-9	10-14		
♀1	8.9	17.9	4.0	(0.0)	1.0	2.0	0.0	0.0	1.0	0.0	4.3	1.0
♀10h	1.7	13.3	1.0	(0.0)	0.0	0.0	0.0	1.0	0.0	0.0	6.0	3.0
♀13	14.1	13.4	3.5	(0.3)	0.5	1.0	0.5	0.5	0.8	0.0	4.0	0.5
♀15	15.9	13.7	9.4	(5.9)	1.2	1.8	0.6	0.0	0.0	0.0	1.7	0.0
♀20	23.2	11.4	8.5	(3.4)	1.5	1.3	1.1	0.0	0.6	0.6	2.7	0.2
♀21	8.3	14.0	4.2	(0.8)	2.5	0.8	0.0	0.0	0.0	0.0	2.0	0.0
♀22h	5.0	12.9	2.9	(1.4)	0.7	0.7	0.0	0.0	0.0	0.0	1.8	0.0
♀23h	35.0	21.2	8.9	(2.2)	1.9	1.9	0.0	0.3	1.7	0.8	3.9	0.0
G_h -average	14.0	14.7	5.3	(1.8)	1.2	1.2	0.3	0.1	0.6	0.2	3.3	0.6
♀3	13.3	12.5	2.5	(0.2)	0.1	0.1	0.2	0.1	0.7	0.5	5.4	0.0
♀5	22.8	12.5	7.5	(1.9)	1.5	1.7	0.8	0.9	0.7	0.0	3.0	0.0
♀10	21.3	10.4	6.5	(1.5)	1.5	1.8	0.3	1.0	0.3	0.3	3.3	0.0
♀17	5.4	11.9	2.1	(0.9)	0.3	0.4	0.3	0.1	0.2	0.0	2.5	0.0
♀22	4.7	8.9	2.1	(0.5)	0.5	1.1	0.0	0.0	0.0	0.0	2.3	0.0
♀23	12.1	23.2	4.5	(1.5)	0.8	0.7	0.4	0.5	0.3	0.0	2.9	0.7
G_1 -average	13.3	13.2	4.3	(1.1)	0.9	2.3	0.7	0.4	0.4	0.1	3.2	0.1
♀26	5.9	21.3	3.2	(1.5)	1.3	0.1	0.1	0.1	0.1	0.0	1.8	0.6
♀41	7.9	16.1	7.9	(1.8)	0.8	0.6	0.5	0.0	0.1	0.0	2.1	0.0
♀47	11.1	19.5	6.1	(3.0)	1.9	0.7	0.3	0.1	0.0	0.0	1.8	0.5
G_2 -average	8.3	19.0	5.7	(2.1)	1.3	0.5	0.3	0.1	0.1	0.0	1.9	0.4
CC with A:	—	.1158	.7541***	.4164	.5305*	.6693**	.4202	.5154*	.5552*	.7569***	.0976	-.3828

Statistical significance : * $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$

majority (97.3%) of them were laid on the undersides of its leaves, and only a fraction of the uppersides of the leaves (1.5%), or on buds and stems (1.2%) by only 3 females (♀ 3, ♀ 5 and ♀ 47).

Seventeen females laid eggs singly and successively on the foliage of crucifers. *El*, a temporally integrated behavior, was composed of 4 component patterns, *laying flight* (*Lf*), *drumming* (*dr*), *pressing abdominal tip* (*pr*) and *oviposition* (*ov*) (OHTANI, 1985; cf. Table 1). As its sequence was often repeated several times, *El* can be represented as $n \cdot (Lf \rightarrow dr \rightarrow pr \rightarrow ov)$. The maximal repeated number (n) was 14 (Table 12). *El* were nearly always followed by *Re*, i.e. it was usual for a female to rest after egg laying. The larger the n becomes, the more widely eggs are scattered, because *laying flight* (*Lf*) were often migratory. This tendency is compatible with 'egg-spreading syndrome' of ROOT and KAREIVA (1984): females tend to lay eggs singly, to follow linear flight paths and to pass over many suitable host plants. There is a higher correlation between the average number of eggs laid per hour and the case number of 2 or more eggs per *El* than between that and the case number of an egg per *El* (Table 12, bottom). Namely, the females which laid eggs successively were apt to lay more eggs.

Time spent for *laying flight* (*Lf*) usually exceeded the duration for the sequence of $dr \rightarrow pr \rightarrow ov$ which lasted less than 5 s. But the sequence $pr \rightarrow ov$ was sometimes longer in ♀ 26 and ♀ 47 (ca. 20 s in the longest case). The omission of *ov*, 'empty oviposition', was sometimes observed in $G_{h,2}$ (only one case in G_1 , Table 12, E). KOBAYASHI (1966) frequently observed in on June 5–9, but we did not from late May to mid July.

Visits (i.e. *dr* or *pr*) to leaves of a non-oviposition plant (*Chenopodium album*) were observed only twice in ♀ 23.

Significant differences between generations were found in D ($G_1 - G_2$) in Table 12 ($p < 0.01$, MANN-WHITNEY's U-test). This means that the females in G_2 are apt to lay only an egg or 2 eggs per *El*. It may be related to the longer average duration for an *El* in G_2 than in G_h or G_1 (Table 12, B), only no statistic significance. We observed that the 3 females in G_2 often rested after laying an egg or 2 eggs.

S-11: *Laying more eggs, females scatter eggs successively. This tendency becomes obscure in G_2 .*

General Discussion

We got 11 sectional conclusions (S-1 – S-11), from which some sexual differences are found.

1. Males continue to seek females

The males in *nectar intake* (Ni) were apt to stay for shorter period on flowers than the females (S-3). The 'restlessness' in males come from the rush toward approaching conspecific individuals, in other words, a mating urge of males.

Other conclusions can be considered from the viewpoint of a mating urge of males. Many males in flight approached whitish objects (S-5), and landed on whitish plants

(S-1), though they can recognize females by a near-ultra violet component of the reflection in their wings (OBARA and HIDAKA, 1968 ; OBARA, 1970). "After a longer passivity of an instinctive behavior pattern, the threshold value of its eliciting stimuli sinks" (LORENZ, 1963 : 42). The male in a longer passivity would see anything whitish as a female.

Males themselves are whitish. Consequently, they are attractive each other. The frequency of interindividual behaviors in males was much higher than in females (S-9). This interaction between males relates to the sedentariness in males (*cf.* OHSAKI, 1980 ; SUZUKI, 1980 ; YAMAMOTO, 1981b). OBARA and HIDAKA (1964) already reported that the *fluttering* (*Ft*) of a resting male attracted other males flying nearby.

Furthermore, as the resting site is higher (S-3), males can find more easily other individuals than females.

2. *Females need males only once*

Unmated female as well as mated ones often exhibit the mate-avoiding behavior (SUZUKI *et al.*, 1977 ; SUZUKI, 1978). OHTANI (1985) reported the *abdomen erecting* (*Ae*) by a starved virgin female during *nectar intake* (*Ni*).

For virgin females which are unprepared for mating (*e.g.* starved, thirsty, soon after emergence), some persistent males will be what should be avoided. For mated females, of course, males are disused. It is all right for females to meet and mate with males only once. If females want to be found by males, they had better jump to males and fly ahead of males. Actually, active *prenuptial flight* (*Pf*), which is called as Type-2 (OHTANI, 1985) distinguishable from Type-1 (SUZUKI *et al.*, 1977), was observed more than Type-1 (12 vs 7) in the field condition (*cf.* Table 11).

For the above reason, females lead the mate-avoiding life. In abundant vegetation, females rested on lower sites where they are less found by males (S-2). *Ascending flight* (*Af*) and *abdomen erecting* (*Ae*) are main mate-avoiding behaviors (S-7). *Wing folding* (*Wd*) and *leaning* (*Le*) are the efforts to be not found by approaching males (S-8). Females avoid more interactions among conspecific individuals than males do (S-9).

3. *Males drive females away out of home habitats*

The duration distribution of *flying* (*FL*) is clearly different between males and females (S-4). As other animals, younger butterflies are more active than the older ones (S-6). There is clear change in the behavior between younger mated females and older ones, but not in males. Younger females avoid males with *Af*, while older females with *Ae* (S-6, S-7). Though *Ae* is a motionless pattern, *Af* is so emigratory that the female keeps to ascend beyond the observer's sight (*cf.* OHTANI, 1985).

SHAPIRO (1970) studied the sex ratio in *Pieris protodice*, observed *Af*, and inferred that *Af* produce a density-dependent emigration of females. SUZUKI (1980) reported the male-biased sex ratio of *P. rapae crucivora* in emergence site. BERNSTEIN (1980) also found the density-dependent changes in sex ratio in *Colias lesbia*, observed female behaviors resembling *Ae* and *Af*, and reported that females on many occasions left their home habitat after encounters with males. Furthermore, YAMAMOTO (1983b)

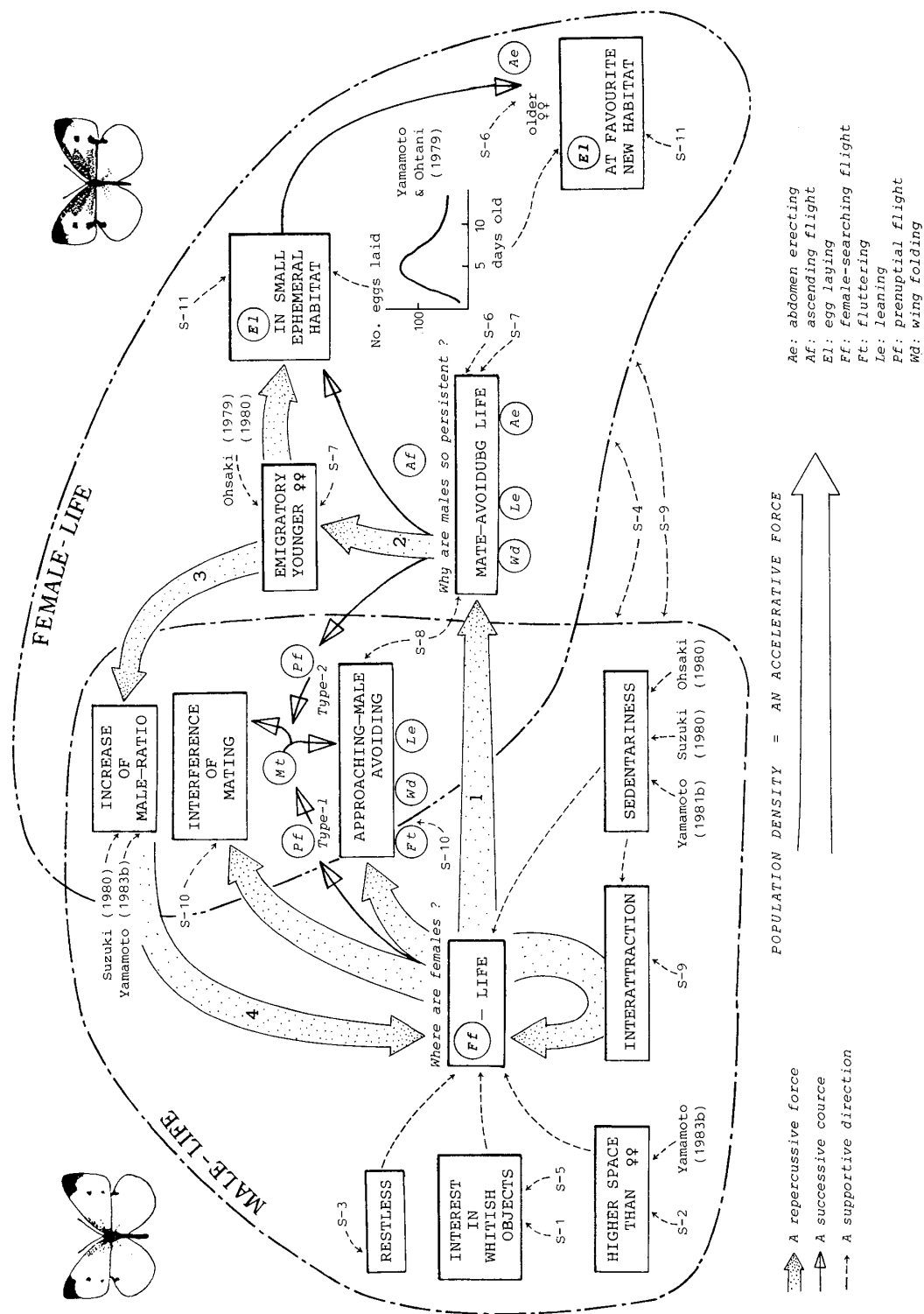


Fig. 4. A concluding schema on the relationship between the female-searching life in males and the mate-avoiding life in females (cf. General Discussion). The each elemental part was supported by 11 sectional conclusions (S-1 - S-11), respectively. The arrows with the number (1-4) form a positive feedback. The process from emigration of younger females with *ascending flight* (Af) to immigration and settlement of older females with *abdomen erecting* (Ae) corresponds to the egg laying curve (YAMAMOTO and OHTANI, 1979).

reported a similar change of sex ratio in *Pieris rapae crucivora* and *P. napi nesis*. From the data of his Table 3, the correlation coefficient between sex ratio and total number of observed individuals (20 or more) was led: $r=0.5941$ ($p<0.02$, $n=17$) in *P. rapae crucivora*, $r=0.4655$ ($0.05<p<0.1$, $n=15$) in *P. napi nesis*. YAMAMOTO (1983b) did not observed *Af* in the latter species.

Having no direct data that *Af* is the mechanism producing the density-dependent changes in sex ratio, we can have a probable prospect: In a dense population, *Af* will increase; the denser a population becomes, the more females will be expelled by males out of home habitats; it would give strongly the male-biased sex ratio.

A male in *female-searching flight* (*Ff*) approaches a female regardless of her conditions. He tries to mate with even the female in copula. This trial is an interference for the mating couple. Mating is accomplished in a home habitat which is under the condition of the male-biased sex ratio. We considered the functions of *wing folding* (*Wd*), *leaning* (*Le*) and *fluttering* (*Ft*) as a countermeasure by the couple to the interference of males (*cf.* OHTANI and YAMAMOTO, 1980). But this countermeasure would be ineffectual in a denser population. The intensive reactions of the pair in copula prolonged the copulation time unwillingly (S-10).

It is unknown how the prolonged copulation affects the female behavior (*egg laying*, *ascending flight etc.*). At least, however, the sedentary tendencies of males in a dense population could function as the power getting younger females to displace.

The above discussion is compatible with an egg-laying curve inferred by YAMAMOTO and OHTANI (1979). Here, we present a preliminary schema (Fig. 4) supported by 11 sectional conclusions. It would be fruitful as working hypotheses, though there are weak points caused by insufficient data, especially on the age and the generation.

Male butterflies always seek females. This well-known and simple habit has another function in a natural population: some emigratory power. Males are not only carriers of gametes, but also accelerators of female emigration.

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摘 要

野外で観察されたモンシロチョウ成虫の行動 II. 主要な行動型の生態学的側面 (大谷 剛・山本道也)

第1報の行動目録(OHTANI, 1985)にある主要な行動型について、生態学的な側面から分析を試みた(行動型のリストはTable 1)。

観察したフィールドは北海道大学の構内(Fig. 1)で、そこで個体追跡したのは31個体である(Table 2)。私たちが採用した「1個体追跡法」では特別な記録用紙(5秒間隔のスケールが横1列に60個並んで5分、全体で1時間のもの)を用いている。記入の手順は次のとおり: 観察している個体の行動が変化したとき、すばやく時計の針の位置を確認、続いて記録用紙の相当する場所に縦線を入れ、すばやく行動型の略号を書き入れる。

「結果および論議」では7節に分けたが、まとまりのある結論に至ったところで、「まとめ」を挿入した。これが斜体で書かれたS-1–S-11である。

S-1: オスは白っぽい植物上で休息し、メスは産卵植物上で休息する傾向がある。

Table 3にはモンシロチョウが休息したときの植物とその回数を示してある。世代ごとに雌雄の休息回数の比率を比較してみると、S-1の傾向が読み取れる。

S-2: オスはメスよりも高い位置で休息する。

Table 3の第3グループは白っぽい植物でも産卵植物でもないが、オスが多く休息するのは丈の高い植物、メスは低い植物の傾向がある。そこで、雌雄各1個体で休息位置の高さを測定(目分量)した例をTable 4にまとめた。同じ植物(アカザ, *C. album* var. *centrorubrum*)でもS-2の傾向が明らかである。

S-3: 吸蜜の際、オスはメスよりも花にとどまる時間が短い。

吸蜜植物に関する情報はTable 5に集めた。吸蜜した回数(V)と総時間(D)に分けてある。各世代のものを総合して平均吸蜜時間(D/V, 右端の欄)を出すと、S-3の傾向が認められた。詳しく見ていくと、S-1, S-2の傾向も存在する。

S-4: 飛翔(FL)の継続時間は、産卵メス、非産卵メス、オスで大きく違い、また、メスの越冬世代(G_n)では第一、第二世代(G_1, G_2)より長くなる傾向にある。

Fig. 2に飛翔の継続時間の分布を示した。探雌飛翔(Ff)、逃避飛翔(Ef)、移動飛翔(Wf)の3つは記

録紙から分けて取り出すのがかなりむずかしいので、Fig. 2 では混ざったままになっている。オスの飛翔の大半は Ff なので、30 秒以上のものが多く、非産卵メスでは、あまり動く必要がないので、短い Wf が多いと考えられる。産卵メスでは産卵植物への移動がやや長い Wf を必要とする。「吸蜜→飛翔」(Fig. 2 右)の場合は「休息→飛翔」(Fig. 2 左)の場合より花から花への短い移動を含むので、分布は左側に偏っている。メスの越冬世代の飛翔時間の長さには春の植物の少なさが関連すると考えられる。

S-5: 飛翔オスは白っぽい物体に引き付けられる。

飛翔中のオスは、枯れ葉・タンポポの綿毛・ネギぼうず・ビンの白い蓋など白っぽいものに興味を示して近づき、ときにはちょっと触ったりする。

S-6: 個体間行動をみると、若い個体は飛翔中の反応が多く、老齢個体では休息中の反応が増える。とくに、老齢メスでは尻あげ反応 (Ae) が増加する。

Table 6 は、個体間行動の観察回数を日齢別にまとめたものである。追尾 (Ch/), 被追尾 (/Ch), 回転 (Gy), 上昇飛翔 (Af) という飛翔中の行動、および、飛び立ち反応 (To), 傾き反応 (Le), 尻あげ反応 (Ae), 翅閉じ反応 (Wd), はばたき反応 (Ft) という休息中の反応は、それぞれ雌雄とも日齢を 7 日で分けると、違いが出てくる。

S-7: 上昇飛翔 (Af) は若い雌雄によって行なわれ、これが若いメスの羽化地からの移出につながるものと考えられる。すなわち、若いメスは老齢メスより Af をするので、定住的なオスに追い出される格好となる。

Af の情報は Table 7 にまとめた。♂11 を除くと、雌雄とも Af をした平均日齢は 3.6 日であり、時間も午前中が多い。表の右側は Af の前後の行動の流れ。Ch → Af → FL の形をとることが多い。また、Af のあと視界から消えた 4 例も示してある (→ oversighted)。

S-8: メスは、接近してくるオスに気づかれなくとも、翅閉じ反応 (Wd) と傾き反応 (Le) をする。オスが気づいて 25 cm 以内に接近すると、メスは尻あげ反応 (Ae) に切り替える。

休息しているメスに頻繁に見られる 3 つの反応が引き起こされる距離を Table 8 に示した。3 つの反応に属さないわずかな動き (twitching) と反応があるべき距離の無反応 (no response) も示してある。Wd と Le の翅の動きが Ae と全く違うので、どちらの反応にすべきか迷う場合もあると考えられる。不完全な反応の例を () 内に示したが、Ae の不完全なものは完全なものより遠い距離で生じているので (中央値, 5.4 cm : 19.3), 判断の迷いが現れたものとみなした。

S-9: 個体間行動が生じる頻度は、3 つの世代ともオスの場合の方がメスよりもずっと多く、オスの活動性の高さを物語っている。各行動型の頻度を世代で比べると、総個体数の変化 ($G_h \lll G_1 \geq G_2$) と必ずしも一致しない場合がある。G₁ と G₂ のオスの行動に差があると予想される。

個体間行動では S-8 で見たように日齢で影響が出るので、少ない老齢個体データを省き、世代間の違いを Table 9 (不活動時の個体) と Table 10 (飛翔時の個体) に分けてまとめた。各世代の比較は、G の観察総時間を 1.00 としたときの比を他世代で出し (Table 9, 10 の m), それで観測数を割ったもの (括弧内の数値) で行なった。また、総観測数に対する % でも比較した。

S-10: 交尾中に接近してくるオスは交尾時間を引き伸ばす原因となるが、飛来するオスが少ないうちは、交尾オスのはばたき反応 (Ft) は追い払う効果をもつ。

交尾に関する情報は、1976 年のデータが少なかったもので、1980 年に同じ北大構内、1981 年に長崎県北松浦郡田平町で追加したものを一緒にして Table 11 に示した。交尾を邪魔された指標として、はばたき反応の回数 (NFt), 結合飛翔に飛び立った回数 (Nbf), 結合飛翔の総時間 (Dbf) を調べたが、交尾時間 (DC) との相関係数は NFt が最も高かった ($r=0.9055$)。しかし、NFt が 25 以下の 18 例で相関係数を出して見ると、 $r=0.2825$ となり、ほとんど相関はないといえる。これを、25 以下ならはばたき反応が飛来オスを追い払っている結果と解釈した。

Fig. 3 の写真は、SUZUKI *et al.* (1977) が報告したスジグロシロチョウの「求愛ホバリング」に似たものとして掲げた。

S-11: メスは多くの卵をつぎつぎと広い範囲に産んでいくが、 G_2 のメスではこの傾向が弱くなる。

17 個体のメスの産卵については Table 12 に示した。1 時間当たりの産卵数 (A), 1 回の産卵行動 (EI) に費やされた平均時間 (B), 1 時間当たりの EI の数 (C), 1 回の EI に産まれた卵の平均数 (D), 1 時間当たりの「空産卵」の数 (E) を調べ、A と B-E との相関係数 (CC) を一番下に示した。C と D の間は、1 回の EI 中に産まれた卵数 (1-14) で、それに相当する 1 時間当たりの例数である。

1 回の EI で 1 個しか産まないときより、2 個、3 個と産む場合の方が相関係数が高い。つまり、EI を始めたとき、何個も産む個体の方が多くの卵を産むようである。また、A, B, D について世代の集計のところを見ると、 G_2 の数値が G_h , G_1 と違っている。

以上の S-1-S-11 を踏まえ、総合考察をして、Fig. 4 に仮想的なモンシロチョウの生活をまとめた。

オスの生活はほとんどすべて「メス探し」にあてられている。しかも、できるだけメスに近いものに引き付けられるために、メスの次によく似ているオス同士で引き合うことになり、これが前から知られている「オスの定住性」につながるものと考えることができる。

一方、メスは交尾のときオスに出合うだけでよく、交尾以外のオスをなるべく避けるようにしている。つまり、「オス避け」または「交尾避け」生活である。そして、若いメスは上昇飛翔 (Af) でオスを避ける傾向にあり、その結果メスは羽化地をどんどん離れていくことになる。そして、老齢になるに従い、尻あげ反応 (Ae) でオスを避けるようになるので、新たな生息地に落ち着くことになる。

このように、オスの生活とメスの生活が組み合わさって、メスを初めの生息地から移動させるという構造を作り出し、それが、すばやく多くの卵をばらまいていく移動中のメスの特性とともに、不安定な環境をうまく利用するモンシロチョウの生活を構成している、と考えられる。

*

本論文では学名が多数出てくるので、読者の便宜のために、以下に和名の対応表 (ABC 順) を掲げる。

<i>Angelica Miqueliana</i>	ヤマゼリ
<i>Apantelles glomeratus</i>	アオムシサムライコマコバチ
<i>Armoracia rusticana</i>	セイヨウワサビ
<i>Artemisia vulgaris</i> var. <i>vulgatissima</i>	ヤマヨモギ (オオヨモギ)
<i>Brassica campestris</i> <i>Napus</i>	アブラナ
<i>Brassica campestris</i> <i>Rana</i>	カブ
<i>Chenopodium album</i>	シロザ
<i>C. album</i> var. <i>centrorubrum</i>	アカザ
<i>Chenopodium ficifolium</i>	コアカザ
<i>Cirsium arvense</i> var. <i>setosum</i>	エゾノキツネアザミ
Compositae	キク科
<i>Colias erate poliographus</i>	モンキチョウ
Cruciferae	アブラナ科
<i>Dactylis glomerata</i>	カモガヤ
Dicotyledoneae	双子葉植物類
<i>Erigeron annuus</i>	ヒメジョオン
<i>Fabriciana adippe pallescens</i>	ウラギンヒョウモン
<i>Geum aleppicum</i>	オオダイコンソウ
<i>Glechoma hederacea grandis</i>	カキドオシ
Gramineae	イネ科
<i>Helianthus tuberosus</i>	キクイモ
<i>Lactuca Scariola</i>	トゲチシャ

Leguminosae	マメ科
<i>Medicago sativa</i>	ムラサキウマゴヤシ (アルファルファ)
Monocotyledoneae	単子葉植物類
<i>Paspalum</i>	スズメノヒエ属
<i>Petasites japonicus</i>	フキ
<i>Phytolacca esculenta</i>	ヤマゴボウ
<i>Pieris canidia</i>	タイワンモンシロチョウ
<i>Pieris melete</i>	スジグロシロチョウ
<i>Pieris napi nesis</i>	エゾスジグロシロチョウ (北海道亜種)
<i>Pieris napi japonica</i>	エゾスジグロシロチョウ (本州亜種)
<i>Pieris rapae crucivora</i>	モンシロチョウ
<i>Plantago asiatica</i>	オオバコ
<i>Raphanus raphanistrum</i>	セイヨウノダイコン
<i>Rorippa sylvestris</i>	キレハイヌガラシ
<i>Rudbeckia laciniata</i>	オオハングンソウ
<i>Rumex obtusifolius</i>	エゾノギンギシ
<i>Sisymbrium officinale</i>	カキネガラシ
<i>Solanum nigrum</i>	イヌホウズキ
<i>Solidago altissima</i>	セイタカアワダチソウ
<i>Stachys Riederi</i>	イヌゴマ
<i>Sympetrum parvulum</i>	ヒメアカネ
<i>Taraxacum officinale</i>	セイヨウタンポポ
<i>Trifolium pratense</i>	ムラサキツメクサ (アカツメクサ)
<i>Trifolium repens</i>	シロツメクサ
<i>Xanthium Strumarium</i>	オナモミ
<i>Zoysia japonica</i>	シバ